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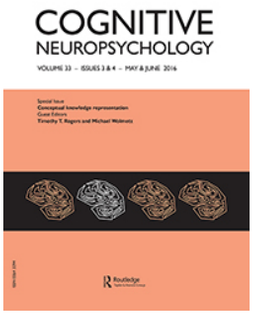

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The neural network for tool-related cognition: An activation likelihood estimation meta-analysis of 70 neuroimaging contrasts

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ABSTRACT

The ability to recognize and use a variety of tools is an intriguing human cognitive function. Multiple neuroimaging studies have investigated neural activations with various types of tool-related tasks. In the present paper, we reviewed tool-related neural activations reported in 70 contrasts from 56 neuroimaging studies and performed a series of activation likelihood estimation (ALE) meta-analyses to identify tool-related cortical circuits dedicated either to general tool knowledge or to task-specific processes. The results indicate the following: (a) Common, task-general processing regions for tools are located in the left inferior parietal lobule (IPL) and ventral premotor cortex; and (b) task-specific regions are located in superior parietal lobule (SPL) and dorsal premotor area for imagining/executing actions with tools and in bilateral occipito-temporal cortex for recognizing/naming tools. The roles of these regions in task-general and task-specific activities are discussed with reference to evidence from neuropsychology, experimental psychology and other neuroimaging studies.

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Tool; tool-use; action; semantic representation; meta-analysis

Introduction

A remarkable feature of human behaviour is the frequent use of various tools to aid actions. The number of objects with which we interact in daily life undoubtedly far exceeds that of other species. Unlike some other species, we do not simply make use of nearby available objects. Instead, we store conceptual and linguistic knowledge about frequently used objects for their efficient use. One can easily pick up scissors to cut a piece of paper or use a stapler to attach several notes to prepare for a meeting. In the physical absence of tools, we can borrow the appropriate tool by referring to it by name. Such stable interactions with objects in everyday life could not have emerged if we had no conceptual, linguistic, or practical knowledge about the objects we frequently use. Yet, we do not fully understand how knowledge and processes related to tools are implemented in our cognitive system or their neural basis.

Case studies in the neurological literature have provided crucial insights. At least two lines of research shed light on tool-relevant cognitive behaviour in humans: (a) investigations of tool recognition and (b) descriptions of action deficits involving tools. Some neurological patients present with a category-specific perceptual deficits for tools (Hillis & Caramazza, 1991; Laiacona & Capitani, 2001; Warrington & McCarthy, 1987). Such patients cannot recognize tools as accurately as they can recognize other categories of objects, such as living things (animals and plants). This stands in contrast to cases of the opposite (animal < tool) dissociation (Basso, Capitani, & Laiacona, 1988; Capitani, Laiacona, Mahon, & Caramazza, 2003; de Renzi & Lucchelli, 1994; Farah, McMullen, & Meyer, 1991; Hart & Gordon, 1992; Warrington & Shallice, 1984). These types of category-specific semantic deficits indicate that some crucial aspect of tool knowledge is anatomically distinct from that of other categories. Another line of evidence about human tool knowledge comes from studies of apraxic patients, who cannot use familiar tools despite having no physical difficulty in moving their body parts and having an intact ability to identify the

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tools (Buxbaum & Saffran, 2002; Buxbaum, Veramonti, & Schwartz, 2000; Gonzalez Rothi & Heilman, 1997; Rosci, Chiesa, Laiacona, & Capitani, 2003). This inability to interact with tools tends to follow lesions in the left parietal lobe and premotor areas, indicating that these areas underpin information about tool-related movements (Barde, Buxbaum, & Moll, 2007; Boronat et al., 2005; Canessa et al., 2008; Goldenberg, 2009).

Motivated by these reports, researchers have used positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) to explore the neural basis of tool cognition. In the domain of perceptual recognition, these attempts have succeeded in identifying a set of neural regions that exhibit category-selective neural responses for tools. Martin, Wiggs, Ungerleider, and Haxby (1996) compared neural responses to pictures of tools and animals while participants engaged in viewing and naming these items. This study found that the left middle temporal gyrus and a medial portion of the occipito-temporal cortex were activated to a greater extent for tools than for animals (Martin et al., 1996). Other studies exploring the category specificity of neural responses in various visuo-perceptual tasks involving familiar objects have amassed consistent evidence that the medial occipito-temporal cortex is more activated in response to tools than to other categories of objects (Chao, Haxby, & Martin, 1999; Devlin et al., 2002; Downing, Chan, Peelen, Dodds, & Kanwisher, 2006). In addition, neuroimaging studies on the category specificity of brain activation frequently reported activations in left frontal, temporal, and parietal regions in response to presentation of tools (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Johnson-Frey et al., 2003; Martin et al., 1996; Perani et al., 1995). However, the involvement of the medial occipito-temporal cortex in tool identification has not been consistently reported in neuroimaging studies related to object perception. Several studies using the same perceptual tasks have not reported any significant activation peaks in the occipito-temporal cortex but tend to highlight the role of frontal and parietal lobe activations in tool perception (Chao & Martin, 2000; Gerlach, Law, Gade, & Paulson, 2000; Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003). It has also been reported that naming tools and naming animals activate distinct areas in the brain, with left middle temporal areas, the inferior parietal lobule, and the premotor area more active when naming tools while animal category evoked higher activation than tools in left lateral-occipital cortex (LOC; Chouinard & Goodale, 2010).

Despite the physical restrictions on body movements imposed in MRI or PET settings, several neuroimaging studies have been able to identify action-related cortical regions that were activated when participants manipulated or imagined using tools. Grafton, Fadiga, Arbib, and Rizzolatti (1996) reported that the imaginary grasping of familiar objects increased activation in the bilateral frontal and parietal areas. Indeed, the left temporoparietal junction (TPJ) exhibited the most prominent activation. In a more recent study, Wadsworth and Kana (2011) asked participants to observe photographs of familiar tools and imagine that they were using them. They reported that imaginary tool use evoked distributed activation in frontal, occipital, and ventral temporal cortices, with the most prominent activation in the left TPJ (Wadsworth & Kana, 2011). Similar activation patterns in the left parietal cortex, extending from the TPJ to the inferior parietal lobule (IPL) and/or angular gyrus (AG) have been reported with imaginary tool-use gestures (Creem-Regehr & Lee, 2005) or conceptual judgments about tool-use actions (Bohlhalter et al., 2009; Boronat et al., 2005; Canessa et al., 2008). These studies have led to the conclusion that the left parietal lobe is crucial for storing and retrieving the body movements necessary for proper object use.

In summary, past neuroimaging studies indicate that different tool-related cognitive processes recruit a variable set of partially overlapping neural structures, and, as such, it is difficult to draw a clear picture of the roles that each region supports. Because individual studies use different cognitive tasks, such as recognition of tools, naming, tool manipulation, or imagining tool-use actions, it is especially hard to clarify whether activated areas contribute to task-general processing (e.g., the concept of tools) or task-specific processing (perceiving, naming, or reacting to the stimulus). Several attempts have been made to locate convergent brain areas in tool-related neuroimaging studies. Johnson-Frey's (2004) seminal review of the neuroimaging studies of human tool-use ability emphasized differentiable roles of posterior temporal and fronto-parietal regions for tool concepts and associated action representations. From slightly a different perspective, Stout and Chaminade (2007) argued that rostral and caudal intraparietal sulcus

(IPS) are evolutionary key areas for complex tool-use and tool-making behaviours. In a quantitative evaluation of the tool-related neuroimaging reports, Lewis (2006) collated reports from 31 neuroimaging studies pertaining to tools and showed comprehensive composite maps of reported activity for tool viewing, naming, hearing tool sounds, and making tool-use actions. This meta-analysis highlighted several key areas including dorsolateral and ventral premotor cortices (DLPMC, vPMC), inferior and middle frontal gyri (IFG, MFG), inferior parietal lobule (IPL), posterior middle temporal gyrus (pMTG), and fusiform cortex (FC). However, there are several methodological issues in this form of meta-analysis. A composite mapping of multiple regions derived from the same group of studies makes it easy to see where the convergence is higher in a particular area than in others. However, with composite mapping, it is impossible to conclude whether the observed set of reported foci is statistically significant. Because of the limited number of anatomically separable areas in the brain, it is always possible that mere random selection of reported regions will yield some degree of convergence. Objective measures to quantitatively analyse a mass of neuroimaging reports using the reported foci (peaks of activation, which are reported in majority of neuroimaging papers) have been proposed. Multi-level kernel density analysis (MKDA) and activation likelihood estimation (ALE) are currently the most popular and frequently used measures of meta-analysis. Both use kernel density estimation but with different assumptions: uniform or Gaussian distribution of the probability of the locations of local maxima around the reported coordinates. The basic idea of the MKDA method, proposed by Wager and colleagues (Wager, Phan, Liberzon, & Tayor, 2003), is to assign each voxel with the number of studies that reported at least one activation peak within a specified (usually 10-mm) radius. This provides an automatic way to derive an activation consistency map. Although this framework is a valid alternative to subjective grouping of activated regions, the assumption of uniform probability density of the kernel used in MKDA is not representative. An activation peak is actually the average location of repetitive observations, which vary across different subjects, normalization procedures, experimental settings, and so on. Thus, the probability of the "true" existence of the activation peak is not distributed uniformly around the reported focus, but can be considered as distributing in a bell-shaped Gaussian function. The ALE meta-analysis, proposed by Turkeltaub and colleagues (Turkeltaub, Eden, Jones, & Zeffiro, 2002), assumes that the probability of the true existence of a given peak activation is distributed in Gaussian form across the nearby voxels and calculates the sum of the probability value (ALE value) derived from all reported foci in a dataset. After Monte-Carlo simulation to determine a null distribution of ALE values and a threshold value for the ALE statistic (i.e., permutations of the location of foci in the dataset and calculating the ALE values in the same manner), one can infer at which voxels the observed ALE value exceeds the hypothetical maximum ALE value that could emerge by chance. The advantage of using this method for meta-analysis in neuroimaging is that it also provides a way to contrast between two groups of studies. In a subtraction (contrast) ALE meta-analysis, two ALE maps from the two datasets are subtracted from each other, and the resultant map of the difference of ALE values is thresholded by essentially the same Monte-Carlo procedure (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012, for details). The foci in each dataset are relocated randomly, and the ALE difference maps are generated in the same way.

The parametric, coordinate-based ALE method has been increasingly used in recent reviews to synthesize and clarify large data sets. For example, Gerlach (2007) analysed the results of 20 functional neuroimaging studies, in which tool and animal items were presented to participants and showed that no area was consistently activated by one category more than the other. Chouinard and Goodale (2010) suggested that the variability of cognitive tasks included in Gerlach's study (naming, object decision, passive viewing, shape/identity matching of objects, classification, picture–identity matching, and semantic categorization) might have led to the inconsistent results. Therefore, they subsequently analysed only the experiments that required "naming" of the visually presented items. Employing this strategy, their meta-analysis succeeded in mapping separate category-specific activation areas for animals and tools. While naming tools generally activated motor regions in frontal lobe, as well as posterior middle temporal gyrus in left hemisphere, naming animals showed greater activation in left medial and ventral frontal regions, lateral occipital cortex, and bilateral posterior fusiform gyri. It is worth noting that these

meta-analyses also indicate that tool-related cortical activation may depend on particular task requirements. This was the core target of our study. Specifically, we utilized the ALE methodology to identify both task-specific and task-general cortical areas related to different aspects of tool knowledge.

In this study we addressed the following questions: (a) What neural regions are implicated in tool-related cognition representation and processing in a task-general manner?; and (b) which neural structures are task-specific? To our knowledge, none of the previous meta-analyses of tool-relevant neural activity have addressed these questions using the recently developed ALE analysis approach (Eickhoff et al., 2009; Eickhoff et al., 2012; Laird et al., 2005; Turkeltaub et al., 2011). For a systematic synthesis and comparison of the literature, we narrowed down our interest to three types of tool-relevant cognitive tasks: recognition, naming, and action. In recognition studies, participants were asked to view tool stimuli while being required to do nothing or perform only perceptual, non-linguistic tasks. In the naming studies, participants were asked to recall (silently or explicitly) the name of the presented tool. Action studies included experiments that asked participants to imagine the body movements required to use each tool. These three tasks were chosen to hold the input modality constant to the visual domain whilst varying the task requirements. Previous studies have examined other modalities of input, such as hearing tool-related sounds (see Lewis, 2006 for review) or imitating tool-use gestures (Goldenberg, 2009 for review). We performed two series of analyses. In Analysis 1, we examined the neural activation patterns estimated for all tasks combined or each of the three different tasks separately (recognition, naming, and action). In Analysis 2, we performed subtraction ALE analyses to differentiate process-specific neural activities. The analyses revealed high similarity between the two perceptual tasks (recognition and naming) while the action task showed a distinct pattern on neural activation. Therefore, in addition to the above two analyses, we ran another series of analyses to examine the commonality and differences between the perceptual (recognition and naming) and motor (action retrieval) groups of tasks, using both the standard and subtraction ALE methods (described as Analysis 3 below).

Method

Study selection

We used the ISI Web of Knowledge (www.isiknowledge.com) to search for relevant studies. The combination of the following three conditions was used to detect candidate papers: including ["fMRI" OR "PET"], ["tool" OR "object"] combined with ["recognition", "recognising", "observation", "observing", "perception", "perceiving", "viewing", "naming", "using", "categorisation", or "use"] appearing in the title or abstract. The papers were further examined in terms of the following inclusion and exclusion criteria: (a) The studies were published in peer-reviewed journals (in English) between 1995 and 2014; (b) the studies reported data obtained via functional neuroimaging with neurologically intact participants using fMRI or PET; (c) one or more conditions reported in the study involved the presentation of familiar tools in the visual domain; (d) the studies reported the coordinates of the local maxima under the tool-presentation condition in either Montreal Neurological Institute (MNI) space (Collins, Neelin, Peters, & Evans, 1994; Evans et al., 1993) or Talairach space (Talairach & Tournoux, 1988); (e) the studies did not focus on sex differences, development, aging, neurological disorders, or other subject-oriented factors. As a result, 56 studies involving 70 contrasts with 474 foci altogether were chosen for the present series of meta-analyses.

The experiments reported in the selected studies were classified into three groups based on type of task. Studies were placed in the "recognition" group if they asked participants either to observe photos or pictures of objects or to perform some kind of non-verbal task that required attending to and recognizing visual stimuli (e.g., same–different judgment, one-back task, or superordinate categorization). Twenty-eight experiments (178 foci) met this criterion. Studies were placed into the "naming" group when the task was to name presented objects silently (covert naming) or explicitly (overt naming). Eighteen experiments (103 foci) fitted the inclusion criterion for this category. Experiments with tasks that required retrieval of tool-use actions were placed in the "action-retrieval" group. Twenty-four experiments (193 foci) were categorized into this group. These studies involved tasks that required the retrieval of learnt actions associated with common tools, such as

planning/imagining/executing tool-use behaviour or judging the similarity between paired tools in terms of their associated actions. To facilitate the random-effect approach of ALE analysis (Eickhoff et al., 2009), a few datasets were combined before analysis. The dataset of three contrasts from Damasio's report (Damasio et al., 1996) and two contrasts from Inoue's report (Inoue et al., 2001) were combined, respectively, as each of them are from the same experiments/subjects (and they in fact reported very similar sets of coordinates). The details of studies and experiments included in the current ALE meta-analysis are listed in Supplementary Table 1.

ALE analysis

We used activation likelihood estimation analysis (ALE) to investigate neural structures that are common and unique to the three types of cognitive processes associated with tools. Two sets of ALE meta-analyses were performed using GingerALE 2.3.5 (Eickhoff et al., 2009; Laird et al., 2005; available at http://brainmap.org/ale/). We primarily followed the ALE procedures proposed by Laird et al. (2005) and Eickhoff et al. (2009). The full-width-half-maximum (FWHM) value for spatial smoothing, based on the number of participants recruited for each study (Eickhoff et al., 2009), ranged from 8.94 to 12.00. A false discovery rate (FDR) of .05 was used to correct *p* values for multiple comparisons. In calculating conjunction map of multiple tasks, we used square (for two-task conjunction) or cube root (for three-task conjunction) of the FDR to ensure the equivalent sensitivity at each voxel to the individual analyses. Only the voxels having significantly higher ALE value in all the interested analyses were regarded significant in the conjunction mapping. We also applied the minor correction to the ALE calculation method proposed by Turkeltaub et al. (2011) to minimize potential biases caused by within-experiment or within-subject effects (non-additive calculation of ALE value at each voxel, by taking the maximum ALE statistics from multiple values convoluted from nearby activation foci from the same experiment). This correction was introduced to prevent the disproportionate influence of studies that report greater number of foci with lenient thresholding. Thresholds for ALE statistics were determined with the permutation procedure proposed by Eickhoff et al. (2012). Ten thousand permutations of randomizing locations of foci within the cortex were performed to calculate the distribution of activation likelihood under null hypothesis. The areas associated with significant values of activation likelihood were mapped onto an MNI template using MRIcron (http://www.nitrc.org/projects/mricron).

Analysis 1 involved a series of ALE analyses intended to identify process-general activation areas shared by the three types of experiments. We initially conducted an ALE analysis on all 474 peaks extracted from the 70 tool-related experiments from 56 papers. The three analyses were then performed separately on the three task-related subsets of the data. Analysis 2 involved a series of formal subtraction analyses using GingerALE Version 2.3.5 to examine differences among the three maps. We performed subtractions between recognition and naming, recognition and action, and naming and action. To ensure sensitivity in the analysis, we used uncorrected $p = .01$ and minimum cluster threshold of 200 mm^3 in all the subtraction analyses. These analyses revealed high overall similarity between the two "tool identification" tasks: recognition and naming. The only difference was observed in the left Broca45 (the details are described in the next section). Contrasts to action task revealed almost identical patterns of significant clusters. Given such similarity in activation patterns, and judging by the fundamental commonality in the requirement of the tasks (both asking identification of familiar objects), we also performed analysis on the identification task group (recognition + naming combined) and compared it with the motor task group (action) to identify credible neuroanatomical commonalities and distinctions between the perceptual and motor tasks (Analysis 3).

Results

Analysis 1: Standard ALE analysis

Figure 1A presents the results of the ALE analysis performed on all 474 foci. It visualizes the areas that are predicted to activate in association with various tool-related tasks in general. The areas include large portions of the left frontal and parietal regions, posterior temporal, and the bilateral occipito-temporal cortices. Specifically, large volumes of voxels with significant activation likelihoods were observed in the left MFG/

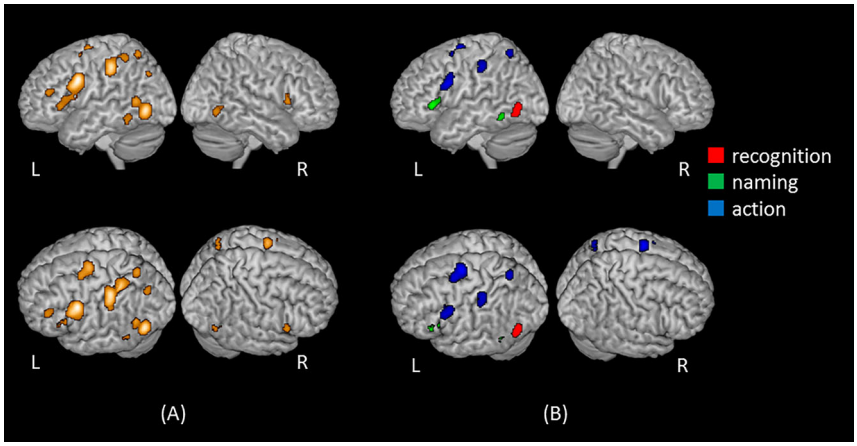

Figure 1. (A) Estimated activation maps by activation likelihood estimation (ALE) meta-analysis on all 70 contrasts from 59 tool-relevant studies. The false discovery rate (FDR) was set at α = .05. The calculated threshold for each voxel in this analysis was $p = .00050$. (B) Activation areas rendered on the surface of the canonical brain. The FDR was set at α = .05. The calculated threshold for each voxel in these analyses were $p = .000026$ for recognition (red), $p = .000025$ for naming (green), and $p = .00014$ for action (blue) analysis. [To view this figure in colour, please see the online version of this Journal.]

IFG (Brodmann area, BA9/44), left IPL extending partly to superior parietal cortex (SPL; BA40/7), left posterior MTG (lateral BA37), left dorsal precentral region (dorsal BA6), left globus pallidus, bilateral occipito-temporal cortices (medial BA37) that involve fusiform and parahippocampal gyri, and other nine relatively smaller clusters in left SPL, bilateral inferior temporal cortex (IT) regions, and parts of middle to inferior frontal gyri in both hemispheres. Figure 1B shows the individual ALE maps for visual tool recognition, naming, and action retrieval, separately. As a group, these individual maps closely correspond to the activation areas shown in the overall analysis (Figure 1A), but indicate which type of task predominantly contributed to the significant activation in the combined analysis.

To estimate common activation regions over different tasks, the conjunction analyses and mapping were also performed as described in the Method section. The results are shown in Figure 2A. The area significant

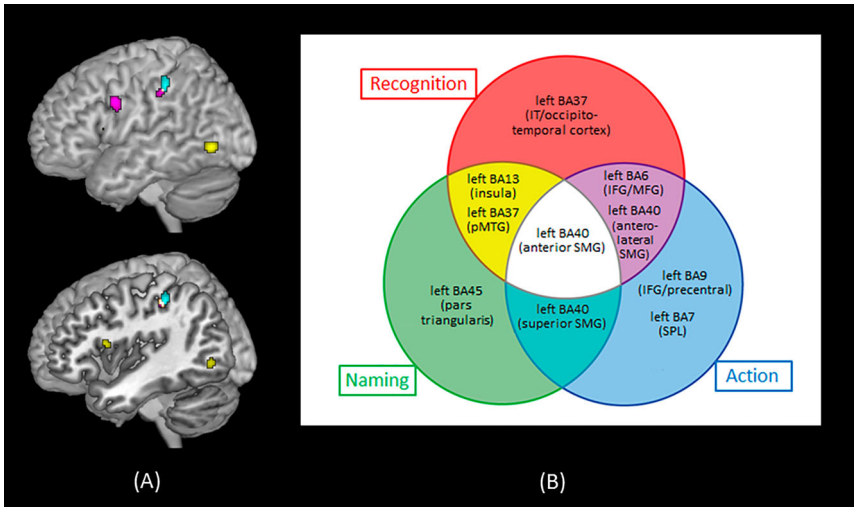

Figure 2. (A) Conjunction activation areas having significant activation likelihood for two or three tasks (with modified FDR threshold for individual task; details in Method). (B) Summary of individual and conjunction ALE analyses in the form of a Venn diagram. The areas with significant likelihood of activation in one or multiple tool-relevant tasks are sorted by Brodmann's labelling (BA = Brodmann area) and classified to the corresponding territory in the diagram. SMG = supramarginal gyrus; SPL = superior parietal lobule; IT = inferior temporal cortex; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; pMTG = posterior middle temporal gyrus. [To view this figure in colour, please see the online version of this Journal.]

in the three-task conjunction is shown in white. This analysis revealed that the left inferior parietal lobule (BA40) is likely to activate in any of the three tasks. The left posterior MTG (BA37) is shown to activate in both recognition and naming. Anterior part of left insula (BA13) has also shown significant likelihood of activation in these two tasks, though the cluster size is small (152 mm^3). The left IFG/MFG (BA6) is indicated to activate in both recognition and action. The areas that are likely to activate in more than one task are summarized in Figure 2B, along with the significant areas from the individual ALE. Supplementary Table 2 lists all the coordinates and associated peak ALE values from Analysis 1.

Analysis 2: Subtraction ALE analysis

The multiple brain slices presented in Figures 3A–3C display the regions with significant task-related differences. The subtraction between recognition and naming (Figure 3A) indicated that only the left pars triangularis (BA45) showed greater activation for naming than for recognition. No area was estimated to show greater activation for recognition than for naming. The subtraction between action and recognition (Figure 3B) estimated that action retrieval was associated with higher activation likelihood than for recognition in the left superior frontal gyrus (BA6). No area was indicated to have higher activation likelihood for recognition than action. The subtraction of action and naming (Figure 3C) resulted in a pattern that was similar to the pattern that emerged from the recognition–action comparison. The left dorsal frontal (BA6) area is more likely to be activated for action retrieval than for tool naming, whereas no area showed the opposite pattern at the statistically significant level.

Analysis 3: Common and dissociable activations for identification and action studies

Given the relative similarity between recognition and naming tasks, and of their differences with action retrieval, we combined the two types of tasks into one group ("identification") and compared this against the action-task data (thereby maximizing the available statistical power to find identification-specific regions). Figure 4 displays the result of standard ALE analysis for this combined group. The significant activation areas for the action groups are also shown again for comparison. The overlapping areas are displayed in white. The largest overlap is at the left supramarginal gyrus (SMG), which is the rostral part of inferior parietal lobule (BA40). The ventro-rostral part of the left precentral gyrus (ventral BA6) is also indicated in both tasks. Figure 4C displays the areas with significant differences in activation likelihood for identification and action. This subtraction indicated that identification of tools was more likely to activate bilateral occipito-temporal cortices (BA37, with the left cluster extending into cerebellum) whereas action retrieval was associated more strongly with activation of the left dorsal premotor (dorsal BA6) region and superior parietal lobule (BA7), as well as the anterior cingulate gyrus (BA24). The locations of peak activation foci provided by this action–identification conjunction and contrast analyses are listed in Supplementary Table 3.

Discussion

This study investigated the neural basis of tool-related knowledge and processing using an ALE meta-analysis of 70 functional neuroimaging contrasts. A series of ALE analyses identified both task-general and task-specific activation patterns. The left dorsal SMG area (BA40) in the inferior parietal lobule was commonly activated in all three tasks (recognition, naming, and action), suggesting that this area codes essential tool information or supports cognitive processes that are shared by all these activities. A similar result and interpretation have been reached in large-scale ALE meta-analyses of multiple cognitive domains (Humphreys & Lambon Ralph, 2015). The ALE maps for recognition and naming tasks were very similar to each other and only differed in a small part of the inferior frontal cortex (BA45), which might reflect the speech production aspect of the naming task. Consequently, action–knowledge tasks were compared to the combination of these two "tool identification" tasks. This direct comparison revealed that tasks involving tool identification were more likely to activate the bilateral medial occipito-temporal areas and left LOC, whereas manipulation tasks were more likely to activate the left fronto-parietal cortices at the dorsal premotor cortex and SPL, as well as anterior cingulate gyrus. Despite the clear distinction between the perceptive (recognition and naming) and motor (action) task groups,

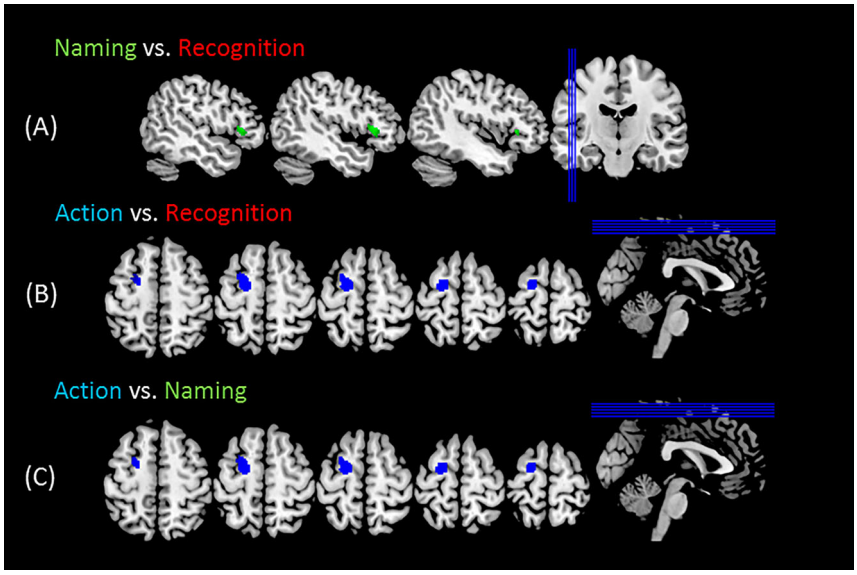

Figure 3. (A) Areas with a significant activation difference between recognition and naming. (B) Areas with a significant activation difference between action retrieval and naming. (C) Areas with a significant activation difference between action retrieval and recognition. [To view this figure in colour, please see the online version of this Journal.]

the conjunction analysis has shown common activation areas in the left anterior SMG (BA40; involving the small portion revealed by three-way conjunction), left anterior-middle IPS (BA40/7), and ventral premotor area extending into pars opercularis (BA6/44). We discuss the roles of these task-general and task-

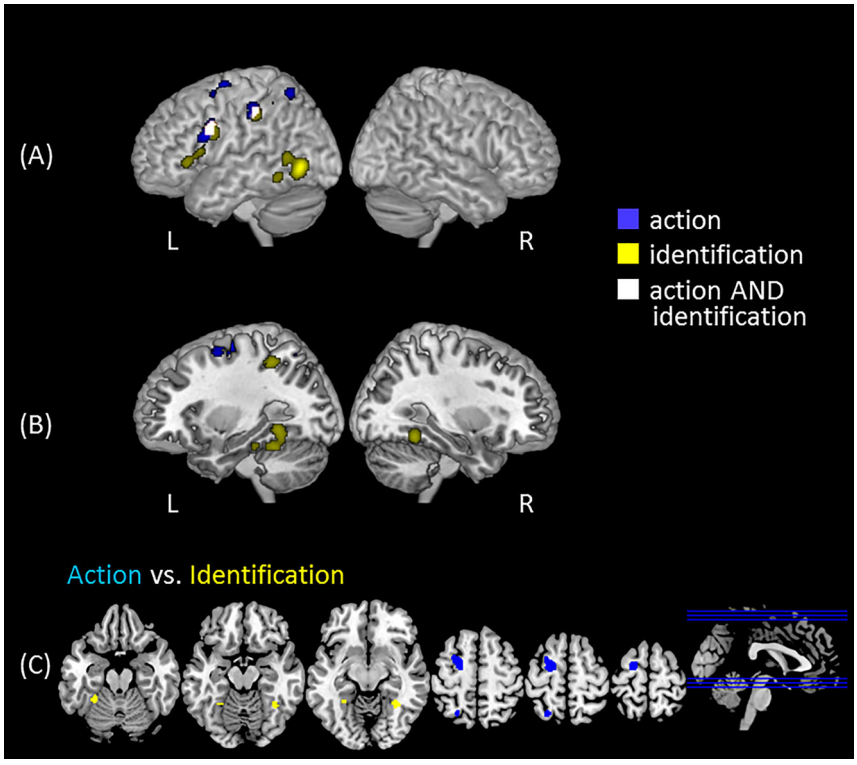

Figure 4. (A, B) Areas with a significant activation likelihood for tool identification and tool-use action retrieval (overlapping regions are shown in white). (C) Areas with a significant activation difference between action retrieval and identification. [To view this figure in colour, please see the online version of this Journal.]

specific activation areas in tool-relevant cognitive activities in the following sections.

Task-general neural activity for tools: Representation or control?

The present meta-analysis revealed that the anterior portion of the left IPL (aSMG) region is active regardless of the specific task requirement that can vary across the tool-related neuroimaging experiments. This was confirmed both by the three-way conjunction test (Analysis 1) and also by the combination of the perceptual and motor task groups (Analysis 3). The convergence of activation across different tasks associated with tool presentation indicates that this region contributes to common processes shared by all of the experimental conditions involved in the studies in question. There are at least two interpretations for the roles of these areas: representing tools or providing general cognitive resource to perform current tasks.

One possible explanation of the contributions of the left IPL in any tool-related task is that this area represents an essential part of the semantic representation for tools. A considerable number of neuropsychological investigations propose that the left IPL stores knowledge about how to manipulate familiar tools. It is widely accepted that damage to this area induces deficient tool use (apraxia: Buxbaum & Saffran, 2002; Gonzalez Rothi & Heilman, 1997). A weak and transient form of this disturbance, observed as a difficulty in recalling knowledge about tool manipulation, has also been observed in neurologically intact participants who receive transcranial magnetic stimulation (TMS) on their left IPL (Ishibashi, Lambon Ralph, Saito, & Pobric, 2011). The contribution of the IPL to tool manipulation probably goes beyond situations that explicitly call for the retrieval of tool-use actions. Another study using TMS on the same area found that TMS over the left IPL induced a transient category-specific naming deficit for manipulable objects, corroborating the notion that the left IPL underpins knowledge about tool manipulation (Pobric, Jefferies, & Lambon Ralph, 2010). This engagement of the IPL in the general context of tool cognition is consistent with the semantic hub-and-spoke framework (Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson, Nestor, & Rogers, 2007). According to this framework, the left IPL is a part of a distributed semantic system coordinated through a transmodal hub and contributes as a modality-specific "spoke", in this case a store of skilled motor movements.

Another possible explanation for the role of the left IPL is that this area provides a general computational resource for the execution of various kinds of tasks, including recognizing and processing general semantic information (Cabeza, Ciaramelli, & Moscovitch, 2012; Humphreys & Lambon Ralph, 2015; Jefferies & Lambon Ralph, 2006). Indeed, in a large-scale meta-analysis of eight different cognitive domains, Humphreys and Lambon Ralph (2015) found that the IPS region extending to dorsal SMG was implicated across all domains including tool manipulation decisions, implying that this region is inherently domain general in nature. Importantly, whilst there was complete overlap in this core IPS region, only the tool-related activation map extended anteriorally and superiorly into SPL regions, consistent with the task-specific findings in this current investigation. Taken together, these data suggest that the core IPL region is inherently domain general in nature and that more task-specific patterns emerge away from this central area, which may well reflect the differential patterns of connectivity across these parietal subregions (Cabeza et al., 2012; Garcea & Mahon, 2014; Humphreys & Lambon Ralph, 2015).

Task-specific neural activity: Tool identification and action retrieval

Subtraction analyses in this meta-analysis revealed contrasting areas implicated in identification (recognition + naming) or action retrieval. The bilateral medial occipito-temporal cortices (involving bilateral BA37) were more likely to be activated by identification than action retrieval with tools, whereas the left dorsal premotor (dorsal BA6) and superior parietal lobule (BA7) exhibited the opposite pattern. These areas are contained within the widely accepted distinction between ventral and dorsal visual pathways (Ungerleider & Mishkin, 1982). According to this theory, information arising in the primary visual cortex follows two distinctive pathways to allow identification of the objects (the "what" pathway) as well as computation of their spatial position (the "where" pathway). This notion was extended by Goodale and Milner (1992), who dubbed the two pathways the ventral "what" and dorsal "how" routes,

reflecting the double dissociation between visual agnosia and optic ataxia.

The notion that the ventral occipitotemporal region is crucial for the extraction of visual information necessary for visual object recognition is very well established. A puzzle for current investigations is why there are graded variations of activation for different categories (e.g., tools, objects, animals, faces, words) across this area (Caramazza & Mahon, 2003; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Mahon & Caramazza, 2009, 2011). Some researchers have suggested that these categorical differences arise from the functional consequences of retinotopic mapping in the early visual pathways. (Felleman & Van Essen, 1991; Hasson et al., 2002; Levy, Hasson, Avidan, Hendler, & Malach, 2001). Specifically, information from the central (foveal) visual field, which contains high-spatial-frequency information, is projected primarily to the posterior fusiform area, whereas peripheral (parafoveal) vision is projected laterally. The proposed functional sequelae of this organization is that object categories that demand extraction of fine visual detail for recognition will tend to rely more heavily on the neural regions that receive foveal input (see Behrmann & Plaut, 2001 for a formal computational implementation of this hypothesis). Alternatively, other researchers argue that this category-sensitive neural organization is hard-wired with our genetic expression and is not developed by the nature of visual input associated with object recognition (Mahon & Caramazza, 2009, 2011). Finally, a more recent computational exploration has shown that, in addition to the visual influences on the posterior fusiform region that are crucial for differentiation of visually similar stimuli including animate items, more medial ventral occipitotemporal cortex (vOT) might respond differentially to tools due to greater connectivity of this region to praxis-related parietal regions (Chen & Rogers, 2015).

The left posterior middle temporal gyrus (lateral BA37/BA19) is significantly activated in the conjunction mapping between recognition and naming in Analysis 1. In Analysis 2, it also showed significant activation likelihood in tool identification (recognition and naming). Although the estimated activation of this area in the subtraction analysis did not reach the default minimum cluster size (200 mm^3) used in the ALE software, a slightly smaller cluster the size of 192 mm^3 was actually indicated in the same contrast with no cluster-size thresholding (the cluster information is included in the Supplementary Table 3). This area has been considered to be a crucial neural region for representation of the non-biological, mechanical motions accompanying tool concepts (Beauchamp, Lee, Haxby, & Martin, 2002, 2003; Chao et al., 1999; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995, 1996) and might act as an additional contributor to the hub-and-spoke representation of semantic knowledge. This region partially overlaps with the human MT+ area (located in the caudal aspects of the superior and middle temporal gyri) that has been designated as the homologue of the monkey MT (middle temporal). Human neuroimaging studies have corroborated that this area responds selectively to particular directions and speeds travelled by visual targets (Amano, Wandell, & Dumoulin, 2009; Dukelow et al., 2001). Damage to this region is known to cause an inability to perceive the motion of visual targets, a neuropsychological condition called akinetopsia or motion blindness (Blanke et al., 2007; Nawrot, 2003; Rizzo, Nawrot, Sparks, & Dawson, 2008). Accordingly, this motion-sensitive area of the left pMTG has been proposed as a key contributor to the representation of mechanical motion of visual objects, including tools (Chao et al., 1999; Kable et al., 2005; Martin et al., 1995, 1996). Studies conducted by Beauchamp and colleagues demonstrated that the motion-sensitive response of the pMTG not only was evoked by the actual movement of tools but also could be elicited, at least to some extent, by static images of tools (Beauchamp et al., 2002, 2003). This selective activation of pMTG to tool motions, however, raises a question: Why does this region show consistent activation in identification of tools but not in use of tools? A possible answer to this question could be that the motion property of a particular tool extracted from its visual representation includes multiple forms of motion that the object can exhibit, each of which can help to different between motion-related objects. For example, a pair of scissors has associated movements that can be observed irrespective if the viewer is using the object (e.g., the opening and closing of the blades), and, in addition, there are other motion features that are integral to the manipulation of the item (the atypical grip applied to this tool). Both aspects are a part of our knowledge of scissors but it is possible that their representation is

divided across posterior temporal and dorsal parietal regions, respectively.

While the bilateral medial occipito-temporal regions and left posterior MTG were observed in the identification–action subtraction analysis, the dorsal premotor and superior parietal regions were highlighted in the opposite contrast (Figure 4). The dorsal premotor region has been discussed in the context of reaching and grasping in both human (Grafton et al., 1996) and monkey studies (Cisek & Kalaska, 2005; Hochermann & Wise, 1991). This is in accordance with the current results as the action tasks asked participants to plan/imagine or to execute concrete physical interaction with tools. However, how the role for this area is different from that for ventral premotor region (activated both for identification and action) is still debated. In a study by Davare and colleagues (Davare, Andres, Cosnard, Thonnard, & Oliver, 2006), transcranial magnetic stimulation applied to dorsal or ventral premotor area in the left hemisphere yielded temporary interference while participants were reaching for an object and configuring proper finger positions to hold (and use) the object, respectively. It is possible that the dorsal premotor area is responsible for guiding hand and arm movements in a larger space to reach and lift a target item, while the ventral premotor is responsible for manipulating the object in hand. In the action retrieval tasks included in this meta-analysis, the explicit instruction to imagine or to execute tool-use actions would encourage more precise action planning including picking up the presented object. This notion is in accordance with the idea that grasping and lifting movements are common among many familiar tools and thus will not contribute to differentiating between different tools. In contrast, finger configuration and movement vary drastically among tools and thus might contribute to fine distinction and identification of different tools.

The parietal regions highlighted in this meta-analysis are located in the superior parietal lobule (SPL) at its posterior part. The posterior part of SPL connecting to occipital lobe have been identified in studies of *optic ataxia* (Pisella et al., 2009; Rossetti, Pisella, & Vighetto, 2003), a neuropsychological condition characterized by an inability to generate object-directed actions such as reaching and grasping, in the absence of motor, somatosensory, visual acuity, or visual-field deficits. Recent studies have offered a functional distinction between two parts of the parietal lobe. Buxbaum and Kalénine (2010) suggested that the bilateral IPS and dorsolateral parieto-frontal regions contribute to rapid and visually guided computation of hand movements during manipulation of both familiar and unfamiliar objects, which they dubbed the "dorso-dorsal pathway" following a previous electrophysiological study of the monkey brain (Rizzolatti & Matelli, 2003). They also proposed that the human "ventro-dorsal pathway", including the left IPL and superior temporal gyrus, contributed to relatively slow and memory-based processing of learnt movements performed in the service of the functional use of familiar tools. This view of two different action systems is consistent with the distinction between optic ataxia and ideational apraxia, respectively. Goldenberg and Spatt (2009) also reported evidence for a crucial dorsal parietal contribution to visually guided planning of object use. In their large-scale investigation of lesion cases, they found that the left IPS and surrounding cortex (close to those identified in the current meta-analysis) were correlated with the degree of participants' deficits in using novel and common objects. This correlation was higher for novel than for common tool tests, indicating that the area is integral for preserving competence in mechanical problem solving. Given these results, Goldenberg and Spatt (2009) suggested that the role of left parietal lobe is to compute the precise spatial relationship among hands, fingers, parts of the tool, and recipient objects. This conclusion would fit with the present meta-analysis findings in that a majority of the action-retrieval studies (20 of 25) explicitly asked participants to imagine or plan tool-use actions whilst the remaining studies also implicitly required action imagery by asking participants to decide whether a specific action (e.g., pinching with fingers) was necessary for the use of each tool (Kellenbach, Brett, & Patterson, 2003) or to evaluate the similarity of the hand/arm movements for a pair of tools (Boronat et al., 2005; Canessa et al., 2008). Successful performance in these tasks is likely to require reasonably detailed and precise mental images of body movements and their relationship with the tools in question.

Conclusion

The present meta-analysis of 70 neuroimaging contrasts identified task-general and task-specific tool-related

neural activations. The left anterior supramarginal gyrus was common across identification (perceptual) and action (motor) tasks. This area would underpin either core representations or cognitive processes that are required across all tool-related tasks. Identification (naming or recognition) of tools was associated with increased activation likelihood in the medial occipito-temporal cortices, which probably reflects extraction of core visual features that are crucial for tool recognition. In contrast, there was heightened activation likelihood for action-retrieval task in the left superior parietal lobule (SPL) and dorsal frontal gyrus, corresponding to the areas within the dorso-dorsal pathway. This circuit is integral to the precise coordination of visuospatial coding of hands, fingers, objects, and their recipients alongside the computation and planning of fine finger and hand movements.

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